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Ion Transport in the Freshwater Zebra Mussel, *Dreissena polymorpha*

JANICE HOROHOV, HAROLD SILVERMAN, JOHN W. LYNN, AND THOMAS H. DIETZ*

Department of Zoology and Physiology, Louisiana State University, Baton Rouge, Louisiana, 70803

Abstract. The blood solute concentration (36 mosm) of pondwater acclimated zebra mussels is among the lowest found in freshwater bivalves. Blood ion concentrations were Na (11–14 m*M*) and Cl (12–15 m*M*), with lesser amounts of Ca (4–5 m*M*), HCO_3 (about 2–4 m*M*), and K (0.5 m*M*). Sodium, Ca and Cl transport rates were 20–30 μeq (g dry tissue · h)$^{-1}$ for pondwater acclimated mussels. The influx of both Na and Cl was stimulated by exogenous serotonin (0.1 m*M*). Sodium transport in zebra mussels was not inhibited by amiloride. Zebra mussels became isosmotic in 30 m*M* NaCl solutions and did not survive beyond a week in 45 m*M* NaCl. Zebra mussels are well adapted to their dilute freshwater habitat, but are more stenohaline than other freshwater bivalves as reflected by their intolerance of elevated ion concentrations in the bathing solution.

Introduction

The zebra mussel (*Dreissena polymorpha*) is the most recent freshwater bivalve introduced into the United States from Europe (Mackie *et al.*, 1989). Unlike other freshwater bivalves, adult zebra mussels attach to solid substrate with byssal threads and may reach densities exceeding $10^5/m^3$. In addition, reproduction involves gametes that are discharged into the water column and develop into free-swimming veliger larvae that may remain planktonic for weeks or months, allowing them to move considerable distances before settling (Mackie *et al.*, 1989; Morton, 1979).

Dreissena has been documented as a serious economic pest because of its propensity to foul raw-water systems, and there is extensive European literature on the ecology and gross morphology (Stanczykowska, 1977; Morton, 1979; Mackie *et al.*, 1989). However, there are few osmoregulatory studies and most physiological studies have focused on methods for control or extermination (Morton, 1979; Mackie *et al.*, 1989).

In a study by Fisher *et al.* (1991), a buffered artificial soft water was found to be lethal to *Dreissena*. Some artificial freshwater solutions are buffered with up to 30 m*M* KH_2PO_4 and 19 m*M* NaOH to maintain neutral pH (Porcella, 1981). This concentration of potassium and sodium and the ionic ratio are exceptional for an artificial freshwater but the primary solute responsible for the mortality in *Dreissena* is potassium (Fisher *et al.*, 1991). Others have noted that zebra mussel distribution is restricted by salinity (see Morton, 1979; Deaton and Greenberg, 1991). Studies demonstrating that zebra mussels are sensitive to ionic concentration have opened avenues for possible methods of controlling their populations. However, other studies have demonstrated that many fresh-water bivalves are killed by low concentrations of potassium (see Dietz and Byrne, 1990).

This report describes some of the characteristics of ionic and osmotic regulation in the zebra mussel and some conditions limiting their survival. Because of the potential similarities with indigenous bivalves, the basic biology of zebra mussels must be understood to be able to selectively control their numbers or distribution.

Materials and Methods

Animals

Zebra mussels (*Dreissena polymorpha*) were collected from Lake Erie near Cleveland, Ohio, and acclimated to artificial pondwater for a minimum of 5 days (Dietz,

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* Address correspondence to: T. H. Dietz, Dept. Zoology and Physiology, Louisiana State University, Baton Rouge, LA 70803.

1979). Mussels were stored unfed in aerated pondwater at 22 ± 2°C before use. Zebra mussels usually survived 6–8 weeks at 22°C with no mortality. For longer maintenance, mussels were held in pondwater at 16 ± 1°C and subsequently transferred to room temperature for at least 24–48 h ([illegible] usually 5 days) before use in experiments. We normally selected larger specimens for study (2–3.5 cm length) with a dry tissue mass of 15–40 mg.

To avoid contaminating local water systems with zebra mussels or veliger larvae, all acclimation water and animal containers were treated with 1% chlorine bleach for 24 h before being discarded. Mussels were dissected from the shell and dried at 95°C, and weighed before being discarded.

Blood analyses

Blood was collected by heart puncture (Fyhn and Costlow, 1975) and centrifuged 8000 g · min before use. We could routinely collect blood volume equal to 10% of the animal weight. However, the mantle cavity retains more pondwater than other freshwater bivalves and was more difficult to drain. Failure to drain the mantle cavity water in smaller zebra mussels will likely contaminate the blood sample if the syringe needle passes beyond the pericardial region. Total solute was determined by freezing-point depression. Sodium and potassium concentration were determined by flame emission, and calcium was assayed by atomic absorption spectroscopy. Chloride was determined by electrometric titration. The bicarbonate concentration in the blood was measured as CO_2 using a Hach Carle analytical gas chromatograph (Boutilier *et al.*, 1985). The bicarbonate concentrations were not routinely measured but were estimated from aliquots of blood that were equilibrated in air. From previous studies, 95–98% of the CO_2 would be in the form of bicarbonate over the pH range 7.5–8.1 (Byrne *et al.*, 1991).

Ion fluxes

Unidirectional ion influxes (J_i) were calculated by monitoring the disappearance of isotope from the bathing medium using previously described methods (Graves and Dietz, 1982). The animals were removed from their storage containers by cutting the byssal thread with scissors or scraping the thread from the container, not by pulling the thread from the animal. The mussels were rinsed in deionized water for about 30 min and transferred to a small container with the appropriate bathing solution. The animals ordinarily did not reattach with byssal threads during the brief period of study. Bath samples were collected at timed intervals and radioactivity determined by liquid scintillation counting. Net flux (J_n) was calculated from the change in ion concentration in the bathing medium. Unidirectional efflux (J_o) was calculated by difference ($J_o = J_i - J_n$).

The effects of exogenous biogenic amines on ion transport were determined by the addition of monoamines to bring the bathing medium concentration to 0.1 m*M*. Several biogenic amines (dopamine, epinephrine, norepinephrine, octopamine, and serotonin) were tested. All monoamine neurotransmitters were obtained from Sigma Chemical Company (St. Louis, MO).

Data are expressed as mean ± one standard error. The Student's *t*-test was used to compare means with equal variances, and differences were considered significant if $P < 0.05$. Time-course studies and the effects of ion concentrations on mussel blood, where variances were unequal, were analyzed by ANOVA and Scheffe's *F*-test on log transformed data.

Results

The blood composition of *D. polymorpha* acclimated to pondwater (PW) is shown in Table I. Zebra mussels were hyperionic to PW with sodium and chloride being the principal solutes. The measured solutes account for 88% of the total solute but there is an ion deficit ("other") of 5.1 m*M*. From another group of animals, we measured the total solute, all of the major ions and total blood CO_2. We noted that most of the missing solute (70%) was CO_2, probably in the form of HCO_3 at neutral to alkaline pH ("other" 3.7 ± 0.7 m*M*; CO_2 2.6 ± 0.4 m*M*; n = 6) (see Byrne *et al.*, 1991). Blood pH of 7.45 has been measured anaerobically from zebra mussels acclimated to pondwater at 23°C, thus 95% of the CO_2 would exist as HCO_3 (unpub. obs., R. Byrne, SUNY-Fredonia).

The blood solute in *D. polymorpha* is among the lowest recorded for freshwater mussels (see Dietz, 1979). To test their ability to osmoregulate, we challenged the mussels with NaCl added to pondwater and measured the blood ion concentrations after 96 h (Table II). There was a significant ($P < 0.01$) 11.8 m*M* rise in blood Na

Table I

Blood and pondwater ion composition in pondwater acclimated Dreissena polymorpha

Ion	Blood	Pondwater
Total Solute, mosm	36.0 ± 1.0	3.00
Na, m*M*	11.5 ± 1.1	0.70
Ca, m*M*	5.2 ± 0.4	0.40
K, m*M*	0.5 ± 0.0	0.05
Cl, m*M*	14.5 ± 0.5	1.35
Other (HCO_3), m*M*	5.1 ± 0.7	0.20

Mean ± SEM, n = 7. Total solute was rounded to 2 significant figures.

Table II

Blood ion concentration in Dreissena polymorpha *after 4 days acclimation to pondwater containing additional NaCl*

Added NaCl (m*M*)	n	mosm Total	Concentration (m*M*) Na	Ca	Cl	Other
0	15	35 ± 2^{a}	10.9 ± 0.8^{a}	5.1 ± 0.4	12.2 ± 0.9^{a}	6.7 ± 0.9^{a}
15	7	51 ± 1^{b}	22.7 ± 1.7^{b}	4.0 ± 0.5	15.6 ± 0.6^{a}	$8.6 \pm 1.5^{a,b}$
30	9	76 ± 2^{c}	32.3 ± 0.7^{c}	5.2 ± 0.9	24.8 ± 1.3^{b}	13.6 ± 1.6^{b}
45	5	96 ± 3^{d}	41.5 ± 1.7^{d}	5.5 ± 1.0	29.6 ± 3.5^{b}	19.4 ± 3.7^{b}

Mean ± SEM. Total solute was rounded to 2 significant figures. [a,b,c,d] Values within a column with different letters are significantly different, $P < 0.05$ with Scheffe's F-test on log transformed data.

concentration at 15 m*M* NaCl accounting for 74% of the elevated total solute. The animals became isosmotic and isoionic for sodium in the 30 m*M* NaCl PW solution, but were hypoionic for Cl in 30 m*M* and 45 m*M* NaCl supplemented pondwater. Above 15 m*M* NaCl the rise in Na, Cl, and HCO_3 (but notably not Ca) contributed significantly to the rise in the total solute.

The addition of 15 m*M* NaCl to PW did not alter the survival of zebra mussels compared to PW acclimated controls. In contrast, some animals in 45 m*M* NaCl died 24 h after the acute transfer and some mortality occurred in animals placed in 30 m*M* NaCl by the second day. The majority of the zebra mussels were dead after 4 days in 45 m*M* NaCl, so we confined our acclimation studies to 4 days. The high standard error observed in the 45 m*M* NaCl group is an indication that the mussels were under physiological stress (Table II). We have not determined if step-wise acclimation favors survival above 45 m*M* NaCl, but acute transfer resulted in 100% mortality by 7 days (data not shown). The results shown in Table II were from animals that had been freshly collected. Repeating the experiment with animals that had been in the laboratory for over a month gave qualitatively similar results but survival time was reduced (data not shown).

The pronounced change in blood ion concentration when challenged with NaCl suggested these animals turn over salts at a rapid rate. This hypothesis was supported by the high ion fluxes measured in *D. polymorpha* (Table III). The PW acclimated animals were in a steady state for Na, Cl and Ca ($J_i = J_o$). The variability of ion fluxes was relatively high, in part, because of the small animal weight (less than 30–40 mg dry tissue) and the difficulty of sampling the bath without disturbing the mussels. Of the measured fluxes, only calcium efflux was significantly higher than Na efflux.

In a separate study, we demonstrated that Na uptake largely was independent of Cl by measuring the unidirectional fluxes from 0.5 m*M* Na_2SO_4 ($J_i = 14.0 \pm 2.7$, $J_o = 19.5 \pm 3.6$ μeq (g dry tissue · h)$^{-1}$, n = 5). In contrast, Cl uptake was significantly dependent on Na. When pondwater acclimated zebra mussels were transferred to 1 m*M* choline chloride, the unidirectional influx was significantly reduced ($J_i = 7.9 \pm 1.5$, $J_o = 49.6 \pm 5.9$ μeq (g dry tissue · h)$^{-1}$, n = 11). Although the Cl efflux was higher than reported in Table III, it was not higher than Cl efflux measured in animals collected at the same time and stored in PW for 2 months in the laboratory (PW controls $J_o = 32.7 \pm 7.5$ μeq (g dry tissue · h)$^{-1}$, n = 8).

The effect of the high transport rates on blood ion concentration in zebra mussels was evident from the time course of acclimation to 45 m*M* NaCl supplemented pond water (Table IV). Within 8 h, total blood solute was

Table III

Unidirectional ion fluxes in pondwater acclimated Dreissena polymorpha

Ion	n	Dry tissue mass, g	μeq (g dry tissue · h)$^{-1}$ Influx	Efflux	Net flux
Sodium	10	0.04 ± 0.00	22.34 ± 1.87	22.91 ± 1.99	-0.57 ± 1.16
Chloride	9	0.04 ± 0.00	24.82 ± 2.96	31.64 ± 5.31	-6.82 ± 4.96
Calcium	9	0.03 ± 0.00	29.04 ± 3.93	30.35 ± 2.37*	-1.31 ± 3.30

Mean ± SEM. * Significantly different than sodium efflux, $P < 0.05$.

Table IV

Change in blood ion [illegible] in Dreissena polymorpha *following acute transfer to pondwater containing 45 mMNaCl*

		mosm	Concentration (mM)				
Hours		Total	Na	Ca	Cl	K	Other
0	6	35 ± 1[a]	13.6 ± 0.2[a]	3.9 ± 0.3	15.0 ± 0.9[a]	0.6 ± 0.0	1.7 ± 0.6[a]
8	3	54 ± 6[b]	25.5 ± 5.0[b]	3.5 ± 0.8	23.3 ± 5.4[a,b]	0.5 ± 0.1	1.4 ± 3.8[a,b]
24	4	80 ± 6[c]	37.7 ± 3.6[c]	4.3 ± 1.1	28.9 ± 4.6[b]	0.4 ± 0.0	8.3 ± 1.8[b]
48	4	96 ± 3[c]	42.7 ± 2.3[c]	3.4 ± 0.7	36.6 ± 2.1[b]	0.3 ± 0.0	12.5 ± 4.2[b]
72	4	100 ± 2[c]	48.4 ± 2.2[d]	2.8 ± 0.3	41.7 ± 1.2[c]	0.3 ± 0.1	6.7 ± 0.7[b]

Mean ± SEM. Total solute was rounded to 2 significant figures. [a,b,c,d] Concentrations within a column having a different letter are significantly different, $P < 0.05$ by Scheffe's F-test on log transformed data.

elevated 54% due to the significant rise in Na that accounted for 62% of the solute gain and by 48 h the zebra mussels were isoionic for Na. The variability of blood ion concentration was high and the rest of the measured ions were not significantly different from controls until 24 h when Cl and HCO_3 became significantly elevated. Calcium and potassium did not change during the 3-day acclimation period. Although chloride was significantly less than Na ($P < 0.05$) on day 3, it was not significantly different from the 45 m*M* acclimation concentration. Elevation of blood bicarbonate concentration ("other") compensated for the Cl anion deficit. Because of the differential time course of changes in the measured blood ions, there was no evidence that the loss of body water due to the acute transfer to the hyperosmotic 45 m*M* NaCl was a predominant factor, although the potential for some water loss does exist.

In previous studies we have shown that the addition of serotonin to the bathing medium stimulated Na transport in other freshwater mussels (Dietz *et al.*, 1982). Serotonin (0.1 m*M*) also significantly elevated Na influx and net sodium flux in zebra mussels (Table V). Most animals displayed considerable motor activity, valve gaping, frequent valve closures, and extension of the foot. These behavioral responses to serotonin are similar in pattern to the response shown by unionids exposed to exogenous serotonin. The hyperextension of the foot and valve closures in *D. polymorpha* frequently caused an elevation of the bath ion concentration due to bleeding. In addition, some animals held in the laboratory for over a month failed to open during the flux study as indicated by fluxes near zero, and were excluded as outliers (fluxes exceeding 3 standard errors of the mean).

Because of the rapid ion turnover, and to prevent significant isotope backflux, unidirectional fluxes were measured over a short time of 1–2 h. We also extended the time of serotonin treatment to 3 h and measured the net Na and Cl fluxes in zebra mussels in PW (Table VI). Serotonin significantly reduced the spontaneous loss of Na experienced by this group of mussels but did not stimulate a net uptake, yet the same mussels experienced a net uptake of Cl. We also exposed zebra mussels to 0.1 m*M* concentrations of several other monoamine neurotransmitters (dopamine, epinephrine, norepinephrine, and octopamine) and measured the net flux of Na and Cl but we saw no significant change relative to control animals (data not shown).

Previous studies have indicated that freshwater mussels differ in the sensitivity of Na transport to amiloride inhibition (Dietz, 1978; McCorkle and Dietz, 1980). The

Table V

*Effects of serotonin (0.1 m*M*) added to pondwater on unidirectional sodium fluxes in pondwater acclimated* Dreissena polymorpha

		μeq (g dry tissue · h)$^{-1}$		
Treatment	n	Influx	Efflux	Net flux
Control	21	29.08 ± 2.15	35.48 ± 2.78	−6.41 ± 1.99
Serotonin	23	40.33 ± 3.83*	31.82 ± 4.82	8.44 ± 4.52*

Mean ± SEM. * Significantly different from controls, $P < 0.02$.

Table VI

*Effect of 0.1 m*M* serotonin in the bathing solution on net ion fluxes in pondwater acclimated* Dreissena polymorpha

	Net flux μeq (g dry tissue · h)$^{-1}$	
Ion	Control	Serotonin
Sodium	−7.12 ± 1.08 (19)	−1.93 ± 1.03 (20)**
Chloride	−1.88 ± 2.05 (19)	10.38 ± 4.93 (19)*

Mean ± SEM with number of animals in parenthesis. Significantly different from controls, $*P < 0.05$, $**P < 0.01$.

unionid bivalve sodium transport system is inhibited by amiloride. In contrast, corbiculid Na transport is not. Sodium transport in *D. polymorpha* was not inhibited by 0.5 m*M* amiloride (Table VII). Some mussels were slow to open their valves and initiate siphoning and this raised the variability of the measured fluxes. However, the amiloride-treated mussels that were observed to be open and siphoning had transport rates that equalled or exceeded the controls.

Table VII

Effects of amiloride (0.5 mM) addition to pondwater on unidirectional sodium fluxes in pondwater acclimated Dreissena polymorpha

	μeq (g dry tissue · h)$^{-1}$		
Treatment	Influx	Efflux	Net flux
Control	22.22 ± 4.24	25.04 ± 2.34	−2.92 ± 4.12
Amiloride	19.00 ± 5.96	30.34 ± 7.33	−11.34 ± 2.29

Mean ± SEM, n = 8.

Discussion

Dreissena polymorpha exhibited several characteristics that were significantly different from the other freshwater bivalves that have been studied. The Cl transport rate was higher than observed in other freshwater mussels and the rate of Na transport is equaled only by the fingernail clam *Musculium* (= *Sphaerium*) *transversum* (Dietz, 1979). Chloride transport was double the transport rate of fingernail clams and 10–20× that of unionids. This is the first report in a freshwater mussel of chloride transport being dependent on Na and Cl uptake being stimulated by exogenous serotonin. Preliminary data indicate that both Na and Cl transport also may be stimulated by serotonin in corbiculids (unpub. obs.). Serotonin has been reported to stimulate only sodium transport in unionid bivalves (Dietz *et al.*, 1982).

The blood of PW acclimated zebra mussels has significantly less total solute than other mussels and was composed primarily of NaCl with only about 2–4 m*M* HCO_3. Organic solutes contribute little to the total solute of freshwater mussels (Hanson and Dietz, 1976). The ionic composition in zebra mussel blood is similar to a Canadian unionid, *Anodonta grandis simpsoniana*, but differs from most other unionids in that they contain a combination of Na, Cl, and HCO_3 (Dietz, 1979; Byrne and McMahon, 1991). Corbiculid blood composition is largely NaCl at about twice the concentration found in *D. polymorpha*. *Corbicula fluminea* also has twice the calcium concentration as the zebra mussel (Dietz, 1979; Byrne *et al.*, 1989).

Acute transfer of zebra mussels to 45 m*M* NaCl resulted in an elevated blood NaCl concentration within 8 h, but 48 h was required for acclimation. *Corbicula fluminea* rapidly adjust blood total solutes within 12 h after being transferred from freshwater to 5‰ (172 mosm), but volume regulation is incomplete even after 120 h (Gainey, 1978). Zebra mussels became isosmotic and suffered considerable mortality when acutely transferred to NaCl solutions above 30 m*M*. In contrast, unionids become isosmotic above 50 m*M* NaCl and survive 75 m*M* NaCl and corbiculids can tolerate even higher solute concentrations (Dietz and Branton, 1975; Gainey, 1978).

Although *D. polymorpha* displayed high ion turnover rates, they were able to maintain a steady state in dilute pondwater. However, storage of zebra mussels in PW, without food, beyond 2 months led to an increase in mortality. Coincidentally, mussels maintained in the laboratory tended to lose solutes and ion fluxes became more variable, but this phenomenon has not been studied systematically.

Sodium transport in zebra mussels was the same in solutions of either NaCl or Na_2SO_4 indicating an independence from chloride transport. Unionid and corbiculid Na transport are also independent of Cl, using instead an apparent Na/H exchange component (Dietz, 1978; McCorkle and Dietz, 1980). We have not examined the exchange mechanism in zebra mussels. Recent studies have indicated that Na flux across amphibian skin is largely regulated by availability of intracellular protons rather than a directly coupled exchange mechanism (Harvey and Ehrenfeld, 1988; Kirschner, 1988).

This is the first evidence that Cl transport is dependent on Na in a freshwater mussel. These data indicate that there may be a NaCl co-transport system in *D. polymorpha*. This inference was further supported by the stimulation of both Na and Cl uptake by exogenous serotonin. Because we have not measured transepithelial electrical characteristics in zebra mussels, it is premature to speculate on primary or secondary transport mechanisms.

Both *Dreissena* and *Corbicula* have elevated Na transport rates compared to unionids. Zebra mussels share with *Corbicula* the unusual property that sodium transport is insensitive to amiloride (McCorkle and Dietz, 1980). Since *Corbicula* displays a substantial Na/Na exchange component not found in unionids, it is tempting to speculate that zebra mussels also may have a large Na/Na exchange mechanism contributing to the high isotope turnover, but this has not been measured. It is possible that these Na/Na exchange pathways present in some freshwater bivalves are insensitive to amiloride inhibition.

Alternatively, the large Na exchange diffusion component may be a characteristic of recent brackish-water ancestry of *Corbicula* and *Dreissena*. Although they have invaded freshwater independently, both genera contain species that inhabit brackish-water (for review see

McMahon, 1983; M[illegible]kie *et al.*, 1989; Deaton and Greenberg, 1991).

Freshwater an[illegible] are capable hyper-regulators and usually are a[illegible]erate hyperosmotic conditions that would more [illegible]ouble their normal total solute concentration [illegible]aton and Greenberg, 1991; Kirschner, 1991). *Dreissena* is uniquely stenohaline in showing elevated mortality at low solute concentrations (30 m*M* NaCl), and being incapable of surviving an acute transfer to 45 m*M* NaCl beyond a week. We have noted previously that *Corbicula* subjected to a loss of body water will shift Na and Cl out of the blood compartment presumably into the intracellular fluid (Byrne *et al.*, 1989). It is possible that the changes in intracellular ionic composition due to the gain in Na and Cl may be an attempt to preserve cell volume. Such a mechanism would have major limitations. Either the addition of NaCl to the cells or the resultant imbalance in the Na:K ratio could interfere with electrically excitable tissue (nerve, skeletal, cardiac muscle) and may be a critical factor limiting survival of *Dreissena polymorpha.*

Alternatively, Deaton and Greenberg (1991) have noted a correlation between the osmoregulatory capability of bivalves and their ability to mobilize calcium. They suggested that the mode of action of elevated calcium is to regulate membrane permeability. *Dreissena* blood calcium concentration was similar to other freshwater mussels but it remained constant during periods of hyperosmotic stress. Perhaps the critical feature leading to their stenohaline characteristic is their inability to add Ca as an osmolyte to the blood when under stress.

The variability in ion transport and the magnitude of ion losses in some *Dreissena polymorpha* acclimated to pondwater exceed the range found in other freshwater bivalves. Freshwater mussels are normally nocturnally active and tend to gain salts at night and lose ions during the day (Graves and Dietz, 1980; McCorkle-Shirley, 1982). Perhaps *Dreissena* has more pronounced diurnal rhythms of ion transport. Zebra mussels also form byssal threads and the secreted material may be in ionic form contributing to some of the apparent salt losses. Alternatively, *Dreissena* may be more sensitive to starvation conditions imposed by laboratory storage. Further studies are needed to resolve these issues.

The basis for zebra mussels' intolerance of salt loading is of fundamental interest. There have been few studies of salt tolerance in freshwater mussels and these studies provide little insight with regard to the physiological mechanism (Deaton and Greenberg, 1991). From an environmentally sound perspective, an ionic challenge is likely to be too nonspecific and detrimental to all freshwater bivalves to be a suitable method for general control of zebra mussel populations. However, KCl or NaCl may be useful in controlling zebra mussels in a specific case such as freshwater ballast in trans-oceanic vessels. The addition of 5–10% seawater, in this example, would be lethal to adult zebra mussels.

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